

Ecosystem Theory in Relation to Man

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THE CONCEPT OF THE ECOSYSTEM is not only the center of professional ecology today, but it is also the most relevant concept in terms of man's environmental problems. In the past two years the public has seized on the root meaning of ecology, namely "*oikos*" or "house," to broaden the subject beyond its previously rather narrow academic confines to include the "totality of man and environment," or the whole environmental house, as it were. We are witnessing what I have called a historic "attitude revolution" (Odum, 1969, 1970c) in the way people look at their environment for the very simple reason that for the first time in his short history man is faced with ultimate rather than merely local limitations. It will be well for all of us to keep this overriding simplicity in mind as we face the controversies, false starts, and backlashes that are bound to accompany man's attempts to put some negative feedback into the vicious spiral of uncontrolled growth and resource exploitation that has characterized the past several decades.

As recently as ten years ago the theory of the ecosystem was rather well understood but not in any way applied. The applied ecology of the 1960's consisted of managing components as more or less independent units. Thus we had forest management, wildlife management, water management, soil conservation, pest control, etc., but no ecosystem management and no applied human ecology. Practice has now caught up with theory! Controlled management of the human population together with the resources and the life support system on which it depends as a single, integrated unit now becomes the greatest, and certainly the most difficult, challenge ever faced by human society.

As we have seen, an "anthropocentric" definition of the ecosystem might read something as follows: Man as a part of, not apart from, a life-support system composed of the atmosphere, water, minerals, soil, plants, animals, and microorganisms that function together to keep the whole viable. If you would like a more formal definition, I can give you the one I am using in the third edition of *Fundamentals of Ecology* (Odum, 1971), namely: "Any unit including all of the organisms (i.e., the "community") in a given area interacting with the physical environment so that a flow of energy leads to a clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and non-living parts) within the the system is an *ecological system* or *ecosystem*."

Historical Review of the Ecosystem Concept

Although the term ecosystem was first proposed by the British ecologist A. G. Tansley just 35 years ago (1935) the concept is by no means so recent. Allusions to the idea of the unity of organisms and environment (as well as the oneness of man and nature) can be found as far back in written history as one might care to look, and such an idea has been a basic part of many religions, although less so in Christian religions, as recently pointed out by historian Lynn White (1967). Anthropologists and geographers have long been concerned with the impact of man on his environment and early debated the question: To what extent has man's continuing trouble with deteriorated environments stemmed from the fact that human culture tends to develop independently of the natural environment? The Vermont prophet George Perkins Marsh wrote a classic treatise on this theme in 1864. He analyzed the causes of the decline of ancient civilizations and forecast a similar doom for modern ones unless man takes what we would call today an "ecosystematic" view of man and nature. In the late 1800's biologists began to write essays on the unity of nature, interestingly enough in a parallel manner in German, English, and Russian languages. Thus Karl Mobius in 1877 wrote about the community of organisms in an oyster reef as a "biocoenosis," while in 1887 the American S. A. Forbes wrote his classic essay on "The Lake as a Microcosm." The Russian pioneering ecologist V. V. Dokuchaev (1846-1903) and his disciple G. F. Morozov (who specialized in forest ecology) placed great emphasis on the concept of "biocoenosis," a term later expanded to geobiocoenosis (or biogeocoenosis) (*see* Sukachev, 1944), which can be considered a synonym of the word "ecosystem."

No one has expressed the relevance of the ecosystem concept to man better than Aldo Leopold in his essays on the land ethic. In 1933 he wrote: "Christianity tries to integrate the individual to society,

democracy to integrate social organization to the individual. There is yet no ethic dealing with man's relation to the land" which is "still strictly economic, entailing privileges but not obligations." Thus, man is continually striving, with but partial success so far, to establish ethical relationships between man and man, man and government, and, now, man and environment. Without the latter what little progress has been made with the other two ethics will surely be lost. In the context of the 1970 scene Garrett Hardin (1968) says it in another way when he points out that technology alone will not solve the population and pollution dilemmas; ethical and legal constraints are also necessary. Environmental science is now being called upon to help determine a realistic level of human population density and rate of use of resources and power that are optimum in terms of the quality of human life, in order that "societal feedback" can be applied before there are serious overshoots. This requires diligent study of ecosystems, and ultimately, a judgment on the carrying capacity of the biosphere. If studies of natural populations have any bearing on the problem, we can be quite certain that the optimum density in terms of the individual's options for liberty and the pursuit of happiness is something less than the maximum number that can be sustained at a subsistence level, as so many domestic "animals" in a polluted feed lot!

My advanced ecology class recently attempted to determine what might be the optimum population for the state of Georgia on the assumption that someday the state would have to have a balanced resource input-output (i.e., live within its own resources). On the basis of a per capita approach to land use the tentative conclusion was that a density of one person per 5 acres (2 hectares) represented the upper limit for an optimum population size when the space requirements for quality (i.e., high protein) food production, domestic animals, outdoor recreation, waste treatment, and pollution-free living space were all fully considered. Anything less than 5 acres of life support and resource space per capita, it was concluded, would result in a reduction in the individual person's options for freedom and the pursuit of happiness, and accordingly, a rapid loss in environmental quality. Since the 1970 per capita density of Georgia is 1 in 8 acres, and for the United States as a whole, 1 in 10 acres, no more than double the present U. S. population could be considered optimum according to this type of analysis. This would mean that we have about 30 years to level off population growth. The study also suggested that permanent zoning of at least one-third of land and freshwater areas (plus all estuarine and marine zones) as "open space" in urbanized areas would go a long way towards preventing the overpopulation, overdevelopment, and social decay that is now so evident in many parts of the world today.

The results of this preliminary study have been published (E. P. Odum, 1970b; see also the provocative symposium on "The Optimum Population for Britain" edited by Taylor, 1970).

The Two Approaches to Ecosystem Study

G. Evelyn Hutchinson in his 1964 essay, "The Lacustrine Microcosm Reconsidered," contrasts the two longstanding ways ecologists attempt to study lakes or other large ecosystems of the real world. Hutchinson cites E. A. Birge's 1915 work on heat budgets of lakes as pioneering the *holological* (from *holos* = whole) or *holistic* approach in which the whole ecosystem is treated as a "black box" (i.e., a unit whose function may be evaluated without specifying the internal contents) with emphasis on inputs and outputs, and he contrasts this with the *merological* (from *meros* = part) approach of Forbes in which "we discourse on parts of the system and try to build up the whole from them." Each procedure has obvious advantages and disadvantages and each leads to different kinds of application in terms of solving problems. Unfortunately, there is something of a "credibility gap" between the two approaches.

As would be expected, the merological approach has dominated the thinking of the biologist-ecologist who is species-oriented, while the physicist-ecologist and engineer prefer the "black box" approach. Most of all, man's environmental crisis has speeded up the application of systems analysis to ecology. The formalized or mathematical model approach to populations, communities, and ecosystems has come to be known as *systems ecology*. It is rapidly becoming a major science in its own right, for two reasons: (1) Extremely powerful new formal tools are now available in terms of mathematical theory, cybernetics, electronic data processing, etc.; and (2) formal simplification of complex ecosystems provides the best hope for solutions of man's environmental problems that can no longer be trusted to trial-and-error or one-problem-one-solution procedures that have been chiefly relied on in the past.

Again we see the contrast between merological and holological approaches in that there are systems ecologists who start at the population or other component level and "model up," and those who start with the whole and "model down." The same dichotomy is evident in the very rewarding studies of experimental laboratory ecosystems. One class of microecosystems can be called "derived" systems, because they are established by multiple seeding from nature, in contrast to "defined" microcosms which are built up from previously isolated pure cultures. Theoretically, at least, the approaches are applicable to efforts

to devise life-support systems for space travel. In fact, one of the best ways to visualize the ecosystem concept for students and laymen is to consider space travel, because when man leaves the biosphere he must take with him a sharply delimited enclosed environment that will supply all vital needs with solar energy as the only usable input from the surrounding very hostile space environment. For journeys of a few weeks (such as to the moon and back) man does not need a regenerative ecosystem, since sufficient oxygen and food can be stored while CO_2 and other waste products can be fixed or detoxified for short periods of time. For long journeys man must engineer himself into a complete ecosystem that includes the means of recycling materials and balancing production, consumption, and decomposition by biotic components or their mechanical substitutes.

In a very real sense the problems of man's survival in an artificial space craft are the same as the problems involved in his continued survival on the earth space ship. For example, detection and control of air and water pollution, adequate quantity and nutritional quality of food, what to do with accumulated toxic wastes and garbage, and the social problems created by reduced living space are common concerns of cities and spacecrafts. For this reason the ecologist would urge that national and international space programs now turn their attention to the study and monitoring of our spaceship earth. As was the case with Apollo 13, survival becomes the mission when the limits of carrying capacity are approached.

The Components of the Ecosystem

From the energy or trophic standpoint an ecosystem has two components which are usually partially separated in space and time, namely, an *autotrophic component* (*autotrophic* = self nourishing) in which fixation of light energy, use of simple inorganic substances, and the buildup of complex substances predominate; and secondly, a *heterotrophic component* (*heterotrophic* = other-nourishing) in which utilization, rearrangement, and decomposition of complex materials predominate. As viewed from the side (cross section) ecosystems consist of an upper "green belt" which receives incoming solar energy and overlaps, or interdigitates, with a lower "brown belt" where organic matter accumulates and decomposes in soils and sediments.

It is convenient for the purposes of first-order analysis and modeling to recognize six structural components and six processes as comprising the ecosystem:

A. Components

1. *Inorganic substances* (C, N, CO_2 , H_2O , etc.) involved in material cycles.

16 ECOSYSTEM STRUCTURE AND FUNCTION

2. *Organic compounds* (proteins, carbohydrates, lipids, humic substances, etc.) that link biotic and abiotic components.
3. *Climate regime* (temperature, rainfall, etc.).
4. *Autotrophs* or *producers*, largely green plants able to manufacture food from simple substances.
5. *Phagotrophs* (*phago* = to eat) or *macro-consumers*, heterotrophic organisms, largely animals which ingest other organisms or particulate organic matter.
6. *Saprotrophs* (*sapro* = to decompose) or *micro-consumers* (also called *osmotrophs*), heterotrophic organisms, chiefly bacteria, fungi, and some protozoa, that break down complex compounds, absorb some of the decomposition products, and release inorganic substances usable by the autotrophs together with organic residues which may provide energy sources or which may be inhibitory, stimulatory, or regulatory to other biotic components of the ecosystem. (Another useful division for heterotrophs: *biophages* = organisms that feed on other living organisms; *saprophages* = organisms that feed on dead organic matter.)

B. Processes

1. *Energy flow circuits*.
2. *Food chains* (trophic relationships).
3. *Diversity patterns* in time and space.
4. *Nutrient (biogeochemical) cycles*.
5. *Development and evolution*.
6. *Control* (cybernetics).

Subdivision of the ecosystem into these six "components" and six "processes," as with most classifications, is arbitrary but convenient, since the former emphasize structure and the latter function. From the holistic viewpoint, of course, components are operationally inseparable. While different methods are often required to delineate structure on the one hand and to measure rates of function on the other, the ultimate goal of study at any level of organization is to understand the relationship between structure and function. It is not feasible to go into any detailed discussion of these component-processes in this brief introduction, but we can list a few key principles that are especially relevant to human ecology. Figure 1 is a schematic diagram that may be useful in picturing the basic arrangement and functional linkage of ecosystem components.

1. The living (items A 4-6 above) and non-living (A 1-3) parts of ecosystems are so interwoven into the fabric of nature that it is difficult to separate them; hence operational classifications (B 1-6) do

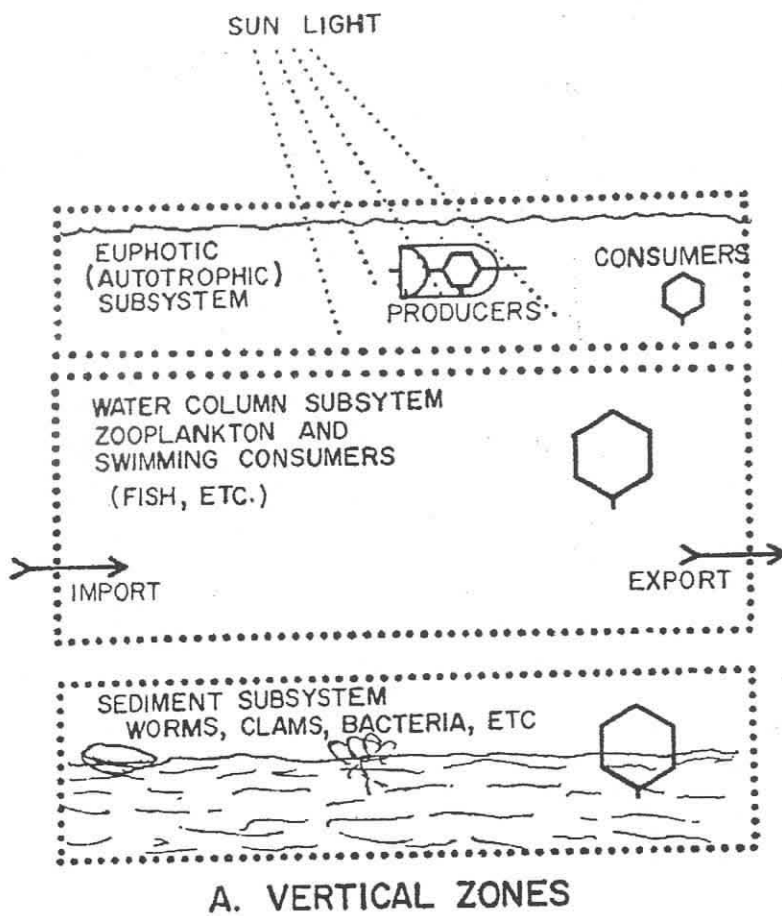
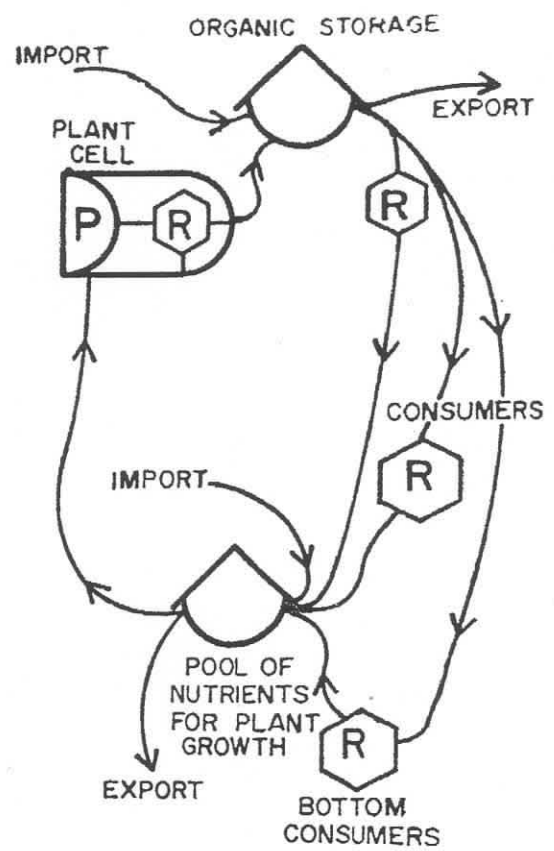
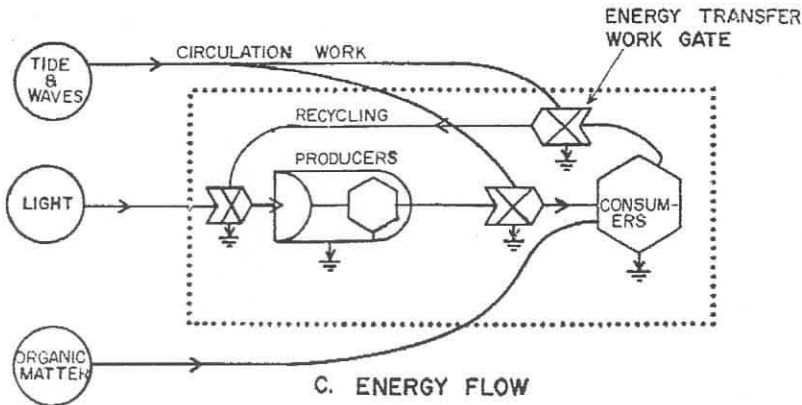


FIGURE 1. Three aspects of the structure and function of ecosystems as illustrated by an estuarine system. A. Vertical zonation with photosynthetic production above (autotrophic stratum) and most of the



B. MINERAL CYCLE

respiration and decomposition below (heterotrophic stratum). B. Material cycle with circulation of plant nutrients upward and organic



matter food downward. **C.** Energy flow circuit diagram showing three sources of energy input into the system. The bullet-shaped modules represent producers with their double metabolism, that is P (production) and R (respiration). The hexagons are populations of consumers which have storage, self maintenance, and reproduction. The storage bins represent nutrient pools in and out of which move nitrogen, phosphorus, and other vital substances. In diagrams B and C the lines represent the "invisible wires of nature" that link the components into a functional network. In diagram C the "ground" symbols (i.e., arrow into the heat sink) indicate where energy is dispersed and no longer available in the food chain. The circles represent energy inputs. The work gate symbols (large X) indicate where a flow of work energy along one pathway assists a second flow to pass over energy barriers. Note that some of the lines of flow loop back from "downstream" energy sources to "upstream" inflows serving various roles there, including control functions (saprotrophs controlling photosynthesis by controlling the rate of mineral regeneration, for example). The diagram (C) also shows how auxiliary energy of the tide (energy subsidy) assists in recycling of nutrients from consumer to producer and speeding up the movement of plant food to the consumer. Reducing tidal flow by diking the estuary will reduce the productivity just as surely as cutting out some of the light. Stress such as pollution or harvest can be shown in such circuit models by adding circles enclosing negative signs linked with appropriate heat sinks to show where energy is diverted away from the ecosystem. Both subsidies (+) and stresses (-) can be quantified in terms of calories added or diverted per unit of time and space. (From E. P. Odum, 1971, after H. T. Odum, Copeland, and McMahan, 1969.)

not make a sharp distinction between biotic and abiotic. Elements and compounds are in a constant state of flux between living and non-living states. There are very few substances that are confined to one or the other state. Exceptions may be ATP, which is found only inside living cells, and humic substances (resistant end products of decomposition) which are not found inside cells yet are characteristic of all ecosystems.

2. The time-space separation of autotrophic and heterotrophic activity leads to a convenient classification of energy circuits into (1) a *grazing* food chain where grazing refers to the direct consumption of living plants or plant parts, and (2) an *organic detritus* (from *deterere* = to wear away) food chain which involves the accumulation and decomposition of dead materials. To build up a stable biomass structure there must be negative feedback control of grazing, a need too often neglected in man's domesticated ecosystems.

3. As is well known, available energy declines with each step in the food chain (so a system can support more herbivores than carnivores; if man wants to keep his meat-eating option open there will have to be fewer people supported by a given food base). On the other hand, materials often become concentrated with each step in the food chain. Failure to anticipate possible "biological magnification" of pollutants, such as DDT or long-lived radionuclides, is causing serious problems in man's environment.

4. It is becoming increasingly evident that high biological productivity (in terms of calories per unit area) in both natural and agricultural ecosystems is almost always achieved with the aid of *energy subsidies* from outside the system that reduce the cost of maintenance (thus diverting more energy to production). Energy subsidies take the form of wind and rain in a rain forest, tidal energy in an estuary (see Fig. 1), or fuel, animal, or human work energy used in the cultivation of a crop. In comparing productivity of different systems it is important to consider the *complete budget*—not just sunlight input.

5. Likewise it is increasingly evident that both *harvest* and *pollution are stresses* which reduce the energy available for self-maintenance. Man must be aware that he will have to pay the costs of added anti-thermal maintenance, or "disorder pumpout" as H. T. Odum (1967, 1970) calls it. It is a dangerous strategy to try to force too much productivity or yield from the landscape (as is being attempted in the so-called "green revolution") because very serious "ecological backlashes" can occur. These may result from: (1) pollution caused by heavy use of fertilizers and insecticides and the consumption of fossil fuels; (2) unstable or oscillating conditions created by one-crop systems; (3) vulnerability of plants to disease because their self-protection me-

chanisms have been "selected out" in favor of yield; and (4) social disorder created by a rapid shift of rural people to cities that are not prepared to house or employ them. (The tragedy here is that industrialized agriculture *can* result in increased food per acre but it can also widen the gap between rich and poor so that there are increasing numbers of people unable to buy the food!)

6. While we generally think of production and decomposition as being balanced in the biosphere as a whole, the truth is that this balance has never been exact but has fluctuated from time to time in geological history. Through the long haul of evolutionary history, production has slightly exceeded decomposition so that a highly oxygenic atmosphere has replaced the original reducing atmosphere of the earth. Man, of course, is tending to reverse this trend by increasing decomposition (burning of fuels, etc.) at the expense of production. The most immediate problem is created by the increase in atmospheric CO_2 , since relatively small changes in concentration can have large effects on the heat budget of the earth.

7. Ecological studies indicate that diversity is directly correlated with stability and perhaps inversely correlated with productivity, at least in many situations. It could well be that the preservation of diversity in the ecosystem is important for man since variety may be a necessity, not just the spice of life!

8. At the population level it is now clear that the growth form of the human population will not conform to the simple sigmoid or logistic model since there will always be a long time lag in the effects of crowding, pollution, and overexploitation of resources. Growth will not "automatically" level off as do populations of yeasts in a confined vessel where individuals are *immediately* affected by their waste products. Instead, the human population will clearly overshoot some vital resource unless man can "anticipate" the effects of overpopulation and reduce growth rates *before* the deleterious effects of crowding are actually felt. Intelligent reasoning behavior seems now to be the only means to accomplish this, as I emphasized at the beginning of this article.

9. Some of the most important "breakthroughs" in ecology are in the area of biogeochemical cycling. Since "recycle" of water and minerals must become a major goal of human society, the recycle pathways in nature are of great interest; there seem to be at least four major ones which vary in importance in different kinds of ecosystems: (1) recycle via microbial decomposition of detritus; (2) recycle via animal excretion; (3) direct recycle from plant back to plant via symbiotic microorganisms such as mycorrhizae associated with roots;

and (4) autolysis, or chemical recycle, with no organism involved. Pathway 3 seems to be especially important in the humid tropics, which suggests that tropical agriculture might be redesigned to include food plants with mycorrhizae.

10. The principles inherent in limiting factor analysis and in human ecology can be combined to formulate the following tentative overview: In an industrialized society energy (power, food) is not likely to be limiting, *but the pollution consequences of the use of energy and exploitation of resources are limiting*. Thus, pollution can be considered the limiting factor for industrialized man—which may be fortunate since pollution is so “visible” that it can force us to use that reasoning power which is supposed to be our special attribute.

Ecosystem Development

Principles having to do with the development of ecosystems, that is, ecological succession, are among the most relevant in view of man's present situation. I have recently reviewed this subject (Odum, 1970a); accordingly a brief summary will suffice here.

In broad view ecosystems develop through a rapid growth stage that leads to some kind of maturity or steady state (climax), usually an oscillating steady state. The early successional growth stage is characterized by a high production/respiration (P/R) ratio, high yields (net production), short food chains, low diversity, small size of organisms, open nutrient cycles, and a lack of stability. In contrast, mature stages have a high biomass/respiration (B/R) ratio, complex food webs, low net production, and high diversity and stability. In other words, major energy flow shifts from production to maintenance (respiration).

The general relevance of the development sequence to land-use planning can be emphasized by the following “mini-model” that contrasts in very general terms young and mature ecosystems:

<i>Young</i>	<i>Mature</i>
Production	Protection
Growth	Stability
Quantity	Quality

It is mathematically impossible to obtain a maximum for more than one thing at a time, so one can not have both extremes at the same time and place. Since all six characteristics are desirable in the aggregate, two possible solutions to the dilemma suggest themselves. We can compromise so as to provide moderate quality and moderate yield on all the landscape, or we can plan to compartmentalize the landscape

so as to maintain simultaneously highly productive and predominantly protective types as separate units subjected to different management strategies. If ecosystem development theory is valid and applicable to land-use planning (total zoning), then the so-called multiple-use strategy, about which we hear so much, will work only through one or both of these cases, because in most cases projected multiple uses conflict with one another.

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Discussion

QUESTION: The "ecology movement" has quite effectively drawn attention to the multitude of environmental problems which confront us, but ecologists seem often to be unaware that we can't do everything, that we must establish some environmental priorities. How do you suggest we should approach problems such as, say, pollution?

DR. ODUM: We have two priorities in regard to pollution abatement that I think we all recognize as major concerns of the "ecology movement" in this country. One priority is to correct mistakes of the past such as attempting to clean up bad pollution and outlawing the dumping of dangerous toxic substances into the environment. A second priority is to prevent further deterioration of the quality of environment. The latter priority, it seems to me, should now receive the greater attention, especially since it is economically more feasible to prevent rather than to clean up. After all, we can live with present levels of pollution, but we will suffer very grievously if pollution and the accompanying waste of resources continues to increase, and sooner or later it will become economically impossible to pay for restoration or recovery of wasted resources. Prevention requires (1) that we "power down" and "recycle" the use of resources and (2) that waste management and land-use planning be given first, not last, consideration in all future industrial, agricultural, and urban development. I indicated some approaches to this in my paper, and I hope that after all the other papers in this symposium have been presented we can come back to future strategies in our final discussion.